THE ALIMENTARY TRACT OF VESPULA MACULIFRONS BUY.

(HYMENOPTERA: VESPIDAE)

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Colonies of the common yellow jacket, *Vespula maculifrons* Buy., are subterranean. The nest is usually in a bank of earth that is elevated from surrounding ground, from which location the drainage of water is good. The normal food for the species consists of juices and pulp of well-ripened fruit, meats, and soft-bodied insects. Unlike the honey-bee, the yellow jacket neither collects nor eats pollen.

Observations made at the very outset of the work upon the gross anatomy of the digestive tract revealed its similarity to that of the honey-bee. The author intends therefore in several instances to compare the alimentary canal of this wasp with the canal of the honeybee. As the basis for comparison the author will use the work of Snodgrass as presented in his "Anatomy and Physiology of the Honeybee" (8).

The material used for the study consisted of seventy-five workers from a single colony in Columbus, Ohio. These were collected in October after a killing frost and about two weeks previous to the hibernation period for the queen and the termination of the colony.

The author wishes to express his sincere appreciation for the helpful suggestions and criticism of Doctor C. H. Kennedy under whose direction this work was undertaken.

TECHNIQUE

Immediately after being killed, the body wall of some of the specimens was cut along the dorsal median line and of others along the ventral median line. The insects were then placed in Kahle's solution for twenty-four hours for fixation of the tissue, after which time they were stored in 70 per cent alcohol. Parts of the tract for sectioning were dissected, stained in borax carmine, cleared in cedar oil and then imbedded in paraffin blocks. Sections three to five microns thick were cut from the block and were then stained with Haemalum (Mayer's newer formula) for nuclei and Fast Green FCF stain for the cytoplasm and cell walls.

THE GROSS ANATOMY OF THE DIGESTIVE TRACT

The alimentary canal is approximately one and one-half times the length of the insect body (Pl. I, Fig. 1). The stomodeum or fore-intestine, which is of ectodermal origin, consists of four structures: namely, the pharynx, oesophagus, crop, and proventriculus.

The Pharynx. The pharynx, situated just posterior to the mouth, is triangular in shape. Around its anterior border is a heavily sclerotized strip. The upper surface of the pharynx possesses a rectangular lamella which is rounded at the end and bears many simple hairs. The pharynx extends dorsally to a point above the level of the attachments of the antennae where it narrows to the diameter of the oesophagus.

The Oesophagus. The osesophagus is a straight narrow tube extending posteriorly from the end of the pharynx through the foramen magnum into the thorax. Through the prothorax and mesothorax the oesophagus is completely surrounded by the thoracic salivary glands. From the mesothorax it progresses in a straight line through the metathorax and the petiole of the insect body, at which point it enters the abdomen. Here the tube widens considerably, forming the crop, which among the bees is termed the honey stomach. (Pl. I, Fig. 1, and Pl. II, Fig. 1.)

The Crop. The size and position of many of the organs in the abdomen vary according to the process of digestion in progress at the time the insect is killed. The crop (Pl. I, Fig. 1) occupies the median part of the first abdominal segment and the anterior portion of the second segment. The crop is capable of great distension; and when it is expanded, the walls of the crop are thin enough to render the food within visible. When the crop is thus enlarged, one can see the proventriculus or gizzard protruding anteriorally into the lumen of the crop. (Pl. II, Fig. 1.)

The Proventriculus. The opening into the proventriculus is X-shaped, indicating the presence of four muscular lips between which the food must pass. The posterior third of the gizzard narrows rapidly to form a short narrow cylindrical peduncle. A tube, the oesophageal valve, projects caudad from the proventriculus through the middle of the ventriculus for approximately one-third the length of the stomach. (Pl. II, Figs. 1 and 2.)

The Ventriculus. The ventriculus or stomach (Pl. I, Fig. 1) is the most conspicuous organ of the entire digestive tract. It varies in respect to position, but in general, it extends from the second abdominal segment to the fifth and along its course forms two loops, one in the second abdominal segment and the other in the third. The ventriculus is annulated, light rings being present where the epithelium within is folded and dark where the epithelium is but a single layer thick and the stomach contents can be seen through it.

A sharp bend occurs at the posterior end of the stomach where the Malpighian tubules enter the pyloric valve.

The Malpighian Tubules. The entrance of the Malpighian tubules into the tract marks the end of the mesenteron or mid-gut and the beginning of the proctodeum or hind-gut. The Malpighian tubules (Pl. I, Figs. 1, 2, 5, 6, and Pl. II, Fig. 1) numbering one hundred or more, are greatly intertwined and wound about the base of the ventriculus and about the intestine. The tubules are very long, being for the most part two-thirds as long as the ventriculus. Each one is attached singly on the circumference of the valve. The distal ends of the tubules lie free in the body cavity.

The Small Intestine. At the end of the pyloric region the tract becomes reduced to about a third of the diameter of the valve. The small intestine (Pl. II, Fig. 1) is marked longitudinally by six light and dark stripes, the light stripes corresponding to the six folds of the epithelium within. The small intestine never follows a straight course but is invariably curved and looped in various ways.

The hind end of the small intestine is indicated by the termination of the previously mentioned stripes, and here the tract becomes greatly enlarged, forming the rectum.

The Rectum. The rectum (Pl. I, Fig. 1, and Pl. II, Fig. 1) like the crop is capable of considerable distention. When not distended the rectum is somewhat depressed; but when it is expanded, it is almost round. The presence of six rectal pads within the rectum is indicated by six white areas shaped like double convex lenses situated longitudinally and extending nearly one-half the length of the rectum. From its middle the rectum tapers to a slender tube which opens at the anus.

There is no decided difference between the external appearance of the alimentary tract of *Vespula maculifrons* and that of the honeybee. A minor difference that was noted is in regards to the rectal pads, which in the honeybee from external appearance are much more narrow and shorter than those in the yellow jacket.

THE HISTOLOGY OF THE ALIMENTARY TRACT

The Oesophagus. The walls of the oseophagus are very muscular, there being a thick layer of both longitudinal and circular muscles. The latter encloses the former. The epithelium is evidenced only by the presence of nuclei scattered within the thick convoluted intima.

The Crop. The structure of the crop (Pl. I, Fig. 3) is fundamentally the same as that of the oesophagus, but the convoluted chitinous intima is much thicker, almost obliterating the lumen. The similarity of structure between these two organs is expected, since they are both of ectodermal origin, being formed by an invagination of the ectoderm of the anterior portion of the embryo, and since the crop is merely an enlargement of the posterior portion of the oesophagus.

The Proventriculus. The proventriculus is of ectodermal origin likewise but differs markedly from the structure of the two previous organs of the stomodeum. The anterior opening of the proventriculus is X-shaped, made so by the presence of four thick columns of longitudinal muscle. (Pl. I, Fig. 4.) The longitudinal muscles of the crop diverge upon reaching the proventriculus and assume two different positions. (Pl. II, Fig. 2.) Some strands turn inward and connect with the thick columnar layers, accompanied in like manner by the circular muscles which form in thick layers around the columns of longitudinal muscles. Other strands of longitudinal muscle continue along the exterior of the proventriculus, making three muscle layers in the proventriculus, a thin layer of longitudinal muscle along the exterior and a thick layer of circular muscles which encircle the third set or inner thick longitudinal muscles. It is from the base of the crop therefore that the order of muscle layers is reversed. This new order, with longitudinal muscles exterior to circular muscles, extends from this point to the end of the alimentary canal.

In the honeybee Snodgrass states that the circular muscles cease at the rear end of the crop and that a new layer of circular muscles arises in the muscular columns of the proventriculus. In *Vespula* these circular muscles are a continuation of the circular muscles of the crop.

Entad to the longitudinal muscle column is a single layer of epithelium evidenced only by nuclei that lie in a straight line, the cell walls not being clearly defined. A thick, dense, and not so convoluted layer of intima lines the lumen of the gizzard. Chitinous projections or spines exist along the intima part of the way through the proventriculus.

The thick layers of longitudinal muscles taper toward the posterior end of the gizzard and finally disappear entirely at the oesophageal valve. The thick layers of circular muscles also taper toward the oesophageal valve but instead of vanishing continue to comprise a part of the musculature of the ventriculus.

The Oesophageal Valve. The oseophageal valve (Pl. II, Fig. 2, OES. V), a prolongation of the epithelium and intima of the proventriculus, projects one-third of the way through the stomach. At the distal end of the prolongation the epithelium of the valve becomes joined to an outgrowth of the epithelium of the ventriculus. This strip of ventricular epithelium one layer thick progresses anteriorally adjacent to the epithelium of the valve until it arrives at a point opposite to the first annular ring, where it turns outward and the cells become attached to the main portion of the epithelium of the stomach.

The Ventriculus. The epithelium of the ventriculus lies in regular sinuous folds, each annular ring visible from the exterior corresponding to a fold in the epithelium. (Pl. III, Fig. 1.) The epithelium is not so irregular as in the honeybee. The epithelium rests on a thin basement membrane. The cells are columnar in shape and rounded at the apex. Those at the tips of the folds projecting into the lumen tend to be larger than the rest of the cells. The nuclei are very conspicuous and lie either in the middle of the cell or toward the base, rarely toward the tip of the cell. Circular muscles encircle the stomach close to the basement membrane and can be found lying between the folds of the epithelium. A layer of longitudinal muscle borders the stomach, and in some instances a thin peritoneum joins these muscles.

Surrounding the food particles in the lumen of the stomach may be seen one to several peritrophic membranes. These membranes are formed from a gelatinous-like secretion of the ventricular epithelium. (Pl. II, Fig. 3.) The free ends of the epithelium projecting into the lumen become filled with the material and become greatly enlarged and club-shaped. The cell wall then bursts, and the secretion is emitted.

The substance thus secreted coagulates on its ental surface next to the food to form the thin film or peritrophic membrane. In the posterior region of the ventriculus there may be six or more peritrophic membranes present at one time. In the anterior portion they are fewer in number. At any time a peritrophic membrane is being laid down in some section of the ventriculus. Some cells are in active secretion while others remain in a different stage of the process. (Pl. III, Fig. 1.) After being formed, the membranes evidently pass along the tract with the food and pass out the anus as a sheath around the feces, which is characteristic of this type of peritrophic membrane that Wigglesworth terms "Type i." (12).

The presence of chitin, detected in the peritrophic membrane of the honeybee by Campbell (3), is the basis for the assumption that the peritrophic membrane must arise from the oesophageal valve, since only epithelium of ectodermal origin has been credited with the ability to secrete chitinous substances. In some insects such as *Sciara* (2), other Diptera, and earwigs (12) the peritrophic membrane is of ectodermal origin, but for the peritrophic membrane in the honeybee and the wasp evidence is sufficient to conclude that the peritrophic membrane arises from the ventricular epithelium, which is generally said to be of mesodermal origin. We must assume then, since chitin has been detected in the peritrophic membrane of the honeybee, that the epithelium of the ventriculus is capable of secreting chitinous material.

The epithelium of the ventriculus secretes not only the substance for forming the peritrophic membrane but also some nucleated bodies which probably contain digestive enzymes. (Pl. II, Fig. 3.)

Regenerative epithelial cells are rare in *V. maculifrons.* A few were found occurring singly or in pairs at the base of a fold in the epithelium. Near the posterior end of the stomach, where the epithelium is less folded and where the cells are longer, a few nidi were found where three or four regenerative cells might occur. (Pl. III, Fig. 3, RC.)

The posterior extremity of the stomach is marked by the entrance of the Malpighian tubules into the tract and by termination of the gelatinous secretion at the inner edges of the cells.

The Malpighian Tubules. The Malpighian tubules are composed of large cells with large and distinct nuclei. The inner surface of the epithelium is smooth, and the cells bulge out into the lumen. These cells rest on a conspicuous basement membrane. (Pl. I, Figs. 2 and 6.)

The Pyloric Valve. Beyond the point of the entrance of the tubules the epithelium is composed of large cuboidal cells with large nuclei. There are both longitudinal and circular muscles present, the former existing as only one layer but the latter increasing in abundance and becoming heavily massed to form a sphincter of the valve. The extremities of the pyloric region are marked by the existence of short and sharp spine-like projections upon the intima on the inner surface of the epithelium. These projections are especially abundant in areas where there appears to be an extra thick layer of intima. In Plate III, Fig. 3, S, the spines have been enlarged beyond their relative size to make them visible upon reproduction.

It is doubtful whether these spines have any definite function. It has been suggested to the author that they may be traces or remnants of the process of the tearing apart of the tissues in this area as the insect passed from the larval stage with a closed hind-gut into the adult stage in which the hind-gut is functional.

The Small Intestine. The epithelium of the small intestine (Pl. III, Figs. 3, 4 and 5) is thrown into six longitudinal folds, occurring as a single layer of cells. It possesses a layer of intima on its free surface. The nuclei are large and round and located near the bases of the cells. Snodgrass records no longitudinal muscle in the small intestinal of the honeybee, but in the yellow jacket there are two muscular layers, an inner layer of circular muscles and an outer one of longitudinal muscles.

The Rectal Valve. This valve is marked by an increase in the number of circular muscles and by a change in shape of the epithelial cells, which become elongate and lie in a double layer. (Pl. III, Fig. 4.)

The Rectum. The longitudinal muscle along the remaining portion of the tract seems to be discontinuous. It is present as an outer layer of muscle along just the anterior portion of the rectum. There is no evidence of a longitudinal muscle again until the tract approaches the anus. The circular muscle exists as a single layer around most of the rectum and then occurs in several layers near the anus. Unlike the rectal pads in *Apis* and the bumblebee (10) there is no lumen. (Pl. III, Figs. 2 and 4.) The cells of the outer layer of epithelial cells are cuboidal and devoid of intima and lie adjacent to the cells of the internal layer, which are large and elongate and possess a heavy chitinous intima. The function of these rectal pads is not definitely known. They may be glands that secrete a substance into the rectum, or they may be structures that draw water from the execrement.

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EXPLANATION OF PLATES

Plate I

Fig. 1. Dorsal view of alimentary tract, showing relative size and position of parts. Malpighian tubules shortened, showing only point of origin.
Fig. 2. Longitudinal section through a Malpighian tubule.
Fig. 3. Cross section through the crop.
Fig. 4. Cross section through the proventriculus.
Fig. 5. Cross section through the pyloric valve. (Semi-diagrammatic.)
Fig. 6. Cross section through a Malpighian tubule.

Plate II

Fig. 1. Alimentary tract removed and straightened, showing relative dimensions of parts.
Fig. 2. Longitudinal section through the oesophageal valve, the valve considerably shortened. (Semi-diagrammatic.)
Fig. 3. Portion of cross section through the ventriculus, showing formation of the peritrophic membrane.

Plate III

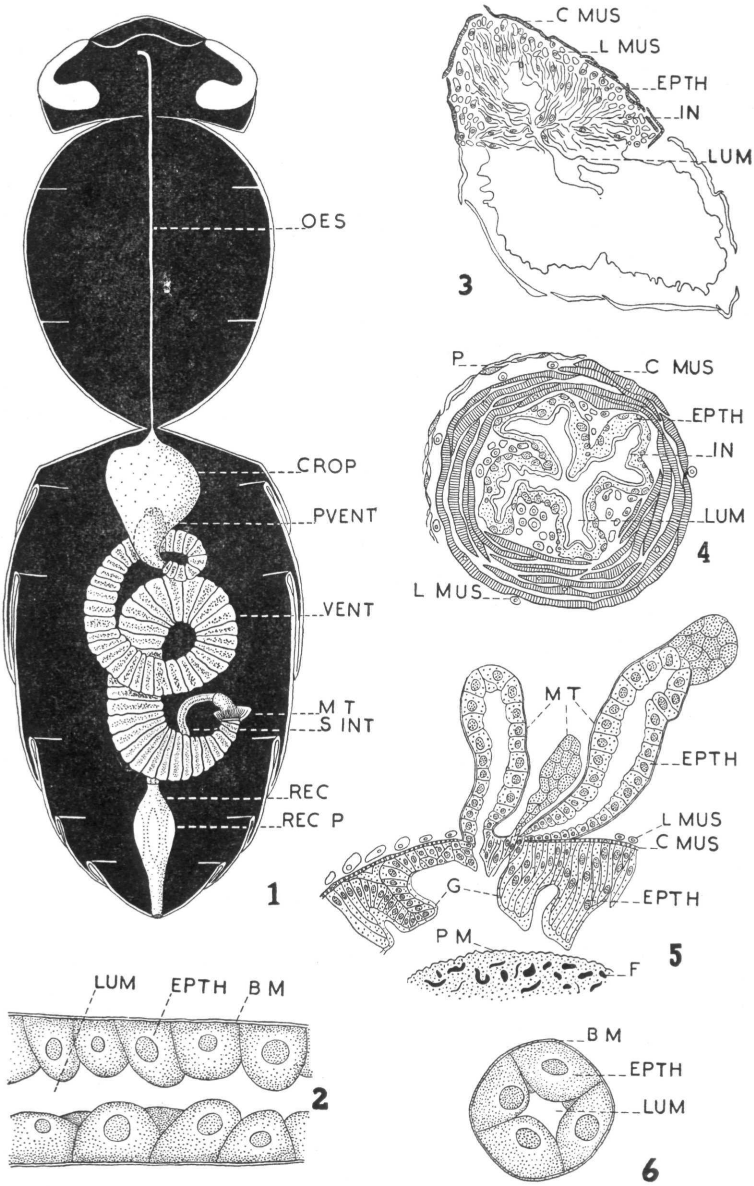
Fig. 1. Longitudinal section through portion of the ventriculus.
Fig. 2. Cross section through mid-section of the rectum.
Fig. 3. Longitudinal section through the pyloric valve.
Fig. 4. Longitudinal section through the rectal valve.
Fig. 5. Cross section through the small intestine.

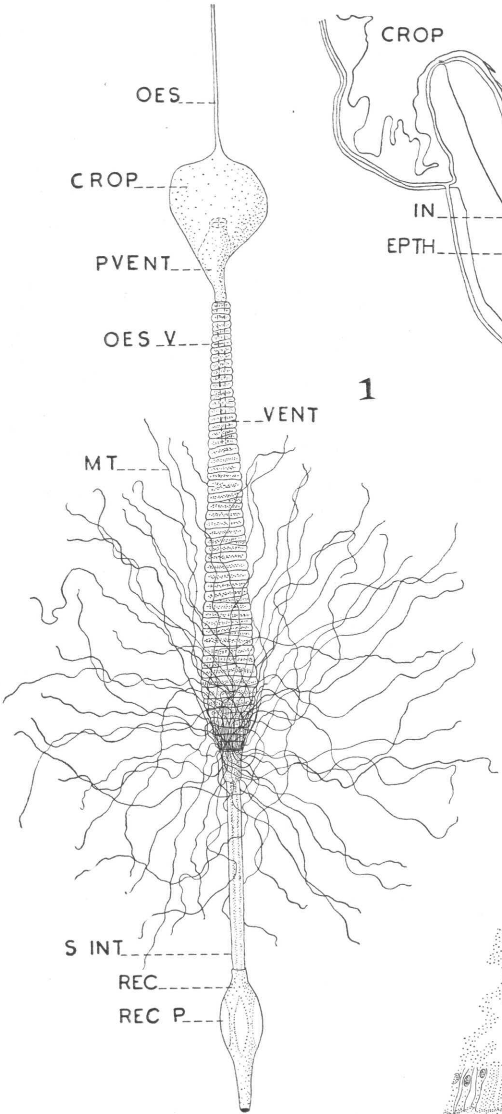
KEY TO THE SYMBOLS USED WITH THE FIGURES

B M—Basement membrane.
C MUS—Circular muscle.
EPTH—Epithelium.
F—Food particles.
G—Secretion of epithelium.
IN—Intima.
L MUS—Longitudinal muscle.
LUM—Lumen.
M T—Malpighian tubule.
OES—Oesophagus.
OES V—Oesophageal valve.
P—Peritoneum.
P M—Peritrophic membrane.
PVENT—Proventriculus.
PYL V—Pyloric valve.
R C—Regenerative cell.
REC—Rectum.
REC P—Rectal pad.
S—Spine.
S INT—Small intestine.
VENT—Ventriculus.

Vespula maculifrons
Robert Thomas Mitchell

PLATE I

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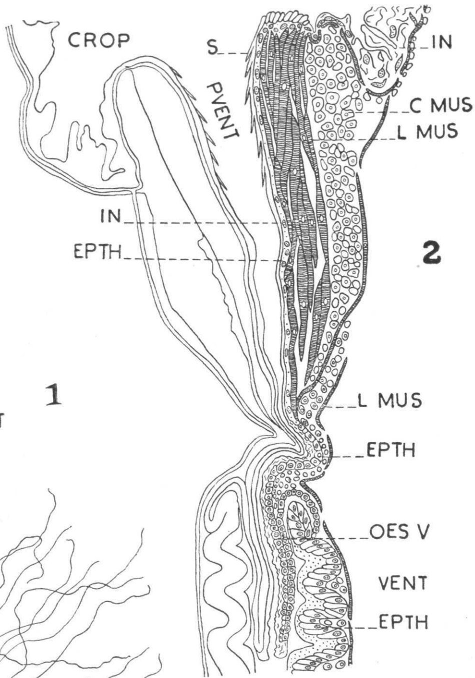
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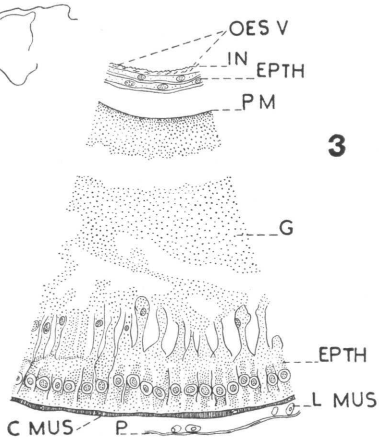
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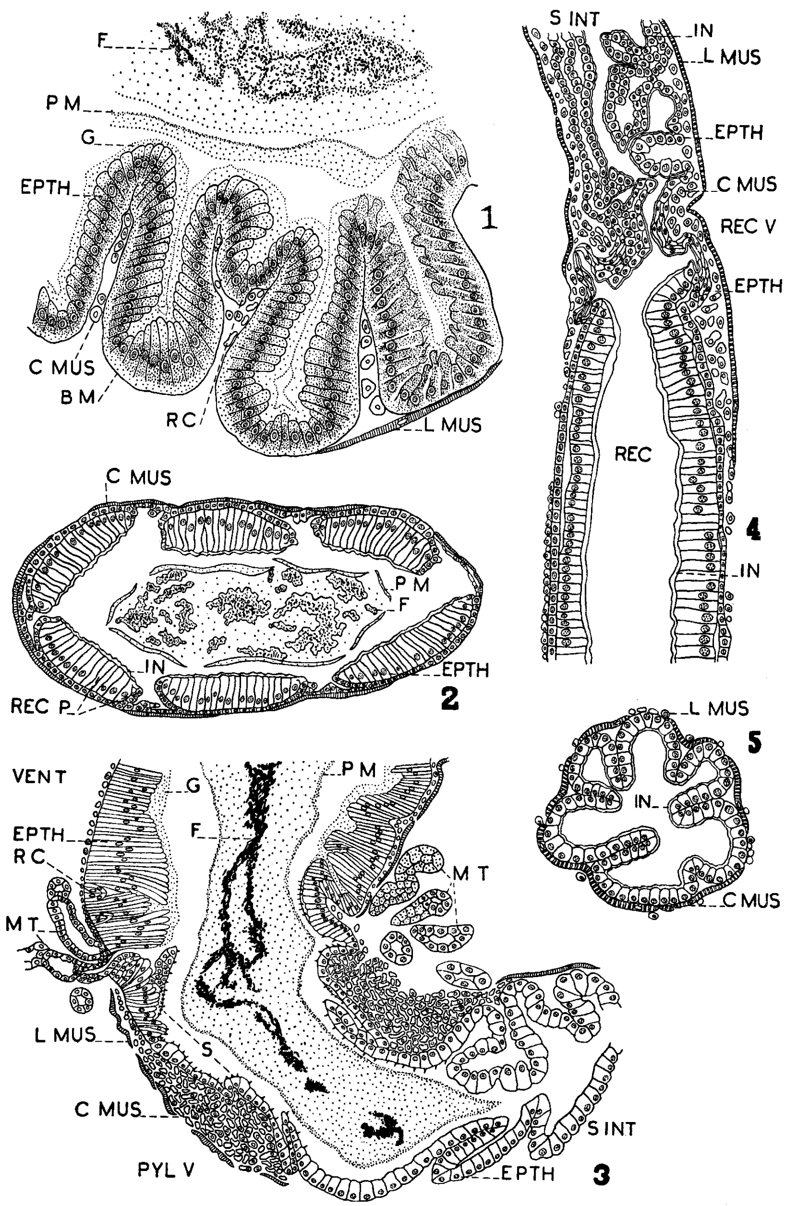
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